ICES Journal of
Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2019), 76(1), 217–231. doi:10.1093/icesjms/fsy117

Original Article

Diel, seasonal, and interannual patterns in mesozooplankton abundance in the Sargasso Sea

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Ivory, J. A., Steinberg, D. K., and Latour, R. J. Diel, seasonal, and interannual patterns in mesozooplankton abundance in the Sargasso Sea. – ICES Journal of Marine Science, 76: 217–231.

Received 6 September 2017; revised 14 June 2018; accepted 10 August 2018; advance access publication 26 October 2018.

Temporal changes in mesozooplankton abundance affect planktonic food web interactions and biogeochemistry. We enumerated mesozooplankton from monthly day and night tows in the epipelagic zone at the Bermuda Atlantic Time-series Study (BATS) site in the Sargasso Sea (1999–2010). Abundances of each taxon were determined using a ZooScan imaging system and microscopy. Generalized linear models were used to determine environmental parameters that best explained abundance patterns. Taxa with pronounced diel vertical migration included euphausiids, amphipods, *Limacina* spp. pteropods, and other shelled pteropods. Taxa with a pronounced spring abundance peak included euphausiids, appendicularians, and *Limacina* spp., while harpacticoid copepods peaked in late summer, and calanoid copepods in late winter/early spring and summer. Many taxa increased in 2003, coincident with a diatom bloom and the largest primary production peak in the time series. Long-term, increasing trends occurred in calanoid and oncaeid copepods, and ostracods, with barnacle nauplii significantly increasing. Sub-decadal-scale climate oscillations and long-term warming may be driving decreases in shelled pteropods and appendicularians. Chaetognath abundance increased in response to increased density of a major prey taxon, calanoid copepods. Calanoid copepods and ostracods increased with increasing water column stratification index and the Atlantic Multidecadal Oscillation index, indicating warmer sea surface temperatures favour these taxa.

Keywords: Atlantic Ocean, BATS, climate change, diel vertical migration, generalized linear models, Sargasso Sea, zooplankton

Introduction

Increasing water temperatures in the North Atlantic Ocean are altering the abundance and spatial distribution of zooplankton species over time (Beaugrand, 2009; Beaugrand *et al.*, 2013), potentially leading to changes in pelagic food web structure and biogeochemical cycling. For example, the geographic distribution of temperate calanoid copepods has moved northwards as subpolar waters warm; abundance of cold water and subarctic calanoids has subsequently decreased while small, temperate calanoid copepod abundance has increased (Beaugrand, 2009; Beaugrand *et al.*, 2013). In the North Atlantic and elsewhere, peaks in zooplankton species abundance are occurring earlier in the season due to warming, leading to trophic mismatches (Richardson, 2008). These changes in zooplankton biogeography, abundance, size distribution, and phenology affect biogeochemical cycling. Specifically, as smaller copepods produce smaller fecal pellets which sink more slowly, the fraction of fecal pellet carbon that reaches depth decreases with copepod size (Stamieszkin *et al.*, 2015). As a result, a system could change to one of primarily recycling rather than exporting (Beaugrand, 2009). Changes in composition and abundance can lead to changes in active transport via diel vertical migration, a component of the biological pump whereby zooplankton transport carbon from the photic zone to depth by feeding in surface waters and metabolizing at depth (Dam *et al.*, 1995; Steinberg *et al.*, 2000). Long-term measurements of plankton species composition and abundance, along with potential environmental controls, are key for predicting planktonic food web and biogeochemical cycling changes in the North Atlantic Ocean due to global climate change.

The Bermuda Atlantic Time-series Study (BATS) in the oligotrophic North Atlantic subtropical gyre was initiated in 1988 to better understand biogeochemical processes on seasonal and decadal time scales and improve predictions of how these processes will be affected by climate change (Steinberg *et al.*, 2001; Lomas *et al.*, 2013). A broad suite of biogeochemical measurements, including process rates, are taken monthly to bimonthly on BATS cruises. Most of the year in the Sargasso Sea, nutrients are low or undetectable in the euphotic zone, although cool winter temperatures and winds deepen the mixed layer and introduce nutrients into the euphotic zone that lead to a spring phytoplankton bloom, usually in February or March (Steinberg *et al.*, 2001; Lomas *et al.*, 2013). In early summer and fall, the mixed layer shoals and nutrient inputs are reduced, which typically results in low phytoplankton and zooplankton biomass (Roman *et al.*, 1993). High chlorophyll concentration coincides with the zooplankton biomass peak in March/April (Steinberg *et al.*, 2001, 2012). Prokaryotic picoplankton usually dominate the phytoplankton (Steinberg *et al.*, 2001), and diatoms have become increasingly rare over the course of a more than two-decade time series (Lomas *et al.*, 2010). The BATS site has experienced a significant increase in sea surface temperature from 1994 to 2011 (Stone and Steinberg, 2014), and longer-term analyses of nearby Hydrostation S (1954 to present) indicate that temperature in the upper 400 m is increasing by ~0.08°C decade^{-1} (Bates, Johnson, and Knap, unpublished). Other long-term changes at the BATS site include increases in chlorophyll *a* biomass and primary production (Saba *et al.*, 2010; Lomas *et al.*, 2013), and in epipelagic zooplankton biomass (Steinberg *et al.*, 2012).

Analyses of Sargasso Sea zooplankton abundance, prior to this work, were largely limited to short-term community or long-term taxon-specific and bulk biomass studies. Early studies showed the major groups of zooplankton between 0 and 500 m were copepods, ostracods, pelagic tunicates, cnidarians (previously "coelenterates"), and chaetognaths (Moore, 1949; Deevey, 1971; Deevey and Brooks, 1971). Copepods represented 70% of the total zooplankton abundance (Deevey, 1971; Deevey and Brooks, 1971), and peaked with other zooplankton taxa in March/April (Moore, 1949; Deevey, 1971; Deevey and Brooks, 1971). More recently, Stone and Steinberg (2014) found salp (gelatinous, pelagic tunicates) abundance (1994–2011) was significantly correlated with primary production, the North Pacific Gyre Oscillation (NPGO), and the Pacific Decadal Oscillation. Mesozooplankton biomass at the BATS site increased 61% from 1994 to 2011, resulting in an increase in the magnitude of export flux via active transport (diel vertical migration), and passive flux of zooplankton fecal pellets (Steinberg *et al.*, 2012). Mesozooplankton biomass change over the 17-year period was positively correlated with primary production, sea-surface temperature, and water column stratification, with weak but significant correlations with several multi-decadal climate indices (Steinberg *et al.*, 2012).

While diel, seasonal, and long-term changes in zooplankton biomass, and some major taxa (salps) have been described, this study provides the first detailed analysis of temporal patterns in major mesozooplankton taxonomic composition and determines which environmental variables drive their composition changes in the Sargasso Sea. Because the taxonomic composition of zooplankton influences food web interactions and export of organic carbon (Steinberg and Landry, 2017), this information is key to predicting effects of global climate change on trophic interactions and biogeochemical cycling.

Material and methods

Zooplankton collection

Zooplankton were collected from the BATS site located in the oligotrophic North Atlantic subtropical gyre (31°40′N 64°10′W), 82 km southeast of the island of Bermuda in the Sargasso Sea. Mesozooplankton sampling for BATS began in April 1994 and is ongoing, with sampling methods described previously in Madin *et al.* (2001) and Steinberg *et al.* (2012). Briefly summarized, mesozooplankton (>200 μm) were collected using a 1-m^2 rectangular frame net with 202 μm mesh. Two replicate day and night, double-oblique tows (ship speed 1–2 nm h^{-1}) were performed on each monthly cruise, and usually on two cruises during each month between January and April. The targeted sampling depth interval was 0–200 m, with the absolute depth recorded by a Vemco Minilog recorder. A General Oceanics mechanical flowmeter measured volume filtered through the net. Samples were split immediately onboard, with half used for biomass measurements and C/N content. The other half sample was preserved in 4% buffered formaldehyde for zooplankton taxonomic identification and enumeration (Madin *et al.*, 2001; Steinberg *et al.*, 2012; Stone and Steinberg, 2014).

Taxonomic analysis

For this study 12 years (1999–2010) of the time series were analysed, with mesozooplankton identified to major taxa (Table 1) similar to Eden *et al.* (2009). Paired *t*-tests were performed on mesozooplankton counts for each taxon (individuals m^{-3}) from tows conducted in 2010 and showed that primary and replicate tows were not significantly different from each other in all taxa. As a result, major taxa from one randomly selected day and night tow from each cruise were enumerated. Overall, 305 tows were analysed from 161 cruises from January 1999 through December 2010. To avoid over estimating delicate vermiform (chaetognaths, polychaetes, and appendicularians) or other taxa (decapods and euphausiids) often broken up in nets or during sample processing, only heads were counted.

Each preserved sample was first size fractioned through a 2000 μm sieve nested in a 200 μm sieve. All animals in the large (>2000 μm) size fraction were identified to major taxon, counted, and measured using the ZooScan optical imagining system at a resolution of 2400 dpi with identification software (Gorsky *et al.*, 2010). The ZooScan produces high-resolution digitized images of a sample and distinguishes one organism from another by detecting space between each individual to create a "vignette" (i.e., Region of Interest). Zooprocessing and PkID programs are then used to create a learning set that the operator develops to properly identify the vignette. The learning set was created by providing 200+ vignettes of individuals within each group to be identified. Program identified vignettes were thoroughly reviewed and identification corrections were made whenever necessary during a validation process for each sample. A Stempel pipette (5 ml) was used to subsample the smaller

Table 1. Major taxa identified from BATS from 1999 to 2010, based on categories used in Eden *et al.* (2009).

Taxonomic categories	Sub categories
Amphipods	Gammarid Hyperiid
Barnacle nauplii	
Brachiolaria	
Chaetognath[a,b]	
Cladocera	
Copepods	Calanoid[a,b] Corycaeidae[a] Harpacticoid Oithonidae[a] Oncaeidae[a] Sapphirinidae
Decapod and mysid	
Doliolid	
Euphausiid	
Heteropod	
Appendicularian[a,b]	
Leptocephali	
Ostracod[a,b]	
Cnidaria	
Polychaete	
Pteropods	*Limacina* spp.[b] Other thecosome Gymnosome

Additional data from 1995 to 1998 were available and included in preliminary analyses for calanoid copepods.

[a] Smaller size fraction (200–2000 μm) identified and enumerated using ZooScan.

[b] Taxa for which additional GLMs were used to evaluate longer-term variables potentially driving interannual changes.

(200–2000 μm) size fraction to obtain a minimum of 200 animals (a 1/2 to 1/2240 split); the most abundant taxa in the small size fraction subsample (Table 1) were enumerated using ZooScan. Because the ZooScan subsample was not large enough to adequately account for less abundant taxa in the small size fraction, a 1/4 to 1/256 split was separately enumerated for these taxa (Table 1), to obtain a minimum of 200 total animals counted, using an Olympus SZX12 stereo microscope under dark and light field illumination.

Statistical analysis

Generalized linear models (GLMs; McCullagh and Nelder, 1989) were used to investigate patterns in abundance (i.e., individuals m^{-3}) of taxonomic groups and their relationship to environmental parameters of interest measured synoptically with each tow. Explanatory variables considered included year, month, day/night, Chl *a* concentration, primary production, raw accessory pigment concentrations for prymnesiophyte and diatom phytoplankton (i.e. 19′-hexanoyloxyfucoxanthin and fucoxanthin, respectively), mesopelagic (300–600 m) temperature extracted from the BATS project website (http://bats.bios.edu/), and prey/predator density whenever applicable. While fucoxanthin is found in prymnesiophytes, chrysophytes, raphydophytes, as well as diatoms (Ansotegui *et al.*, 2001), fucoxanthin is used to primarily indicate diatoms at the BATS site (Lomas *et al.*, 2013). The variables year, month, and day/night were treated as categorical while all others were continuous and standardized: $x_{\mathrm{std}} = (x - \bar{x})/\sigma_x$ (Schielzeth, 2010). Tows with missing explanatory variable data ($n = 38$ out of 305) were assigned a value using linear interpolation of two known cruise values surrounding the missing value. For most cruises, only one measurement of an explanatory variable was missing and no cruises were missing measurements of all explanatory variables. Plots of raw taxa densities consistently showed positively skewed patterns suggestive of a lognormal distribution. Therefore, taxa densities of zero were adjusted by adding a small constant and then all data were transformed using the natural logarithm. Delta GLMs (Aitchison, 1955) were used for rare taxa with densities of zero for 25–89% of the samples (cladocera, gymnosome, leptocephali, and brachiolaria). The delta model has two parts; first a binomial model estimated the encounter probability of the target animal and then a lognormal model estimated the mean density of the animal when it was encountered. Final mean density was calculated as the product of the encounter probability and the mean density estimated from on the nonzero tows. One taxon (phyllosoma—lobster larvae) had densities of zero for ≥90% of the samples and was not analysed.

A suite of 23 models for each taxonomic group were fitted, with each model including year and month (for interpretation of seasonal and interannual patterns), as well as combinations of additional explanatory variables. Fucoxanthin was not included in most of the models considered because the pigment is rare at the BATS site (Krause *et al.*, 2009; Lomas *et al.*, 2013), and preliminary analyses did not show fucoxanthin to be influential. Variance inflation factors were calculated for all explanatory variables and results indicated no evidence of multicollinearity. The model with the most empirical support was identified using Akaike's Information Criterion (AIC; Burnham and Anderson, 2002). From the model receiving the most empirical support, significance of each explanatory variable (or level for the categorical variables) was determined by identifying which βs differed from zero, and directionality of the effects relative to the intercept (β_0) was given by the sign of the estimated parameter (positive vs. negative). Simple linear regressions were used for taxa with a significant year covariate (Table 2) to test for significant long-term abundance increases or decreases.

Comparisons to annualized environmental parameters and climate indices

The most empirically supported GLM for zooplankton density from above for five abundant, major taxa (Table 1) was used to evaluate longer-term variables potentially driving interannual temporal changes. The "year" variable in the favoured GLMs was replaced with 12-month averages of long-term climate variables of interest (Table 3). Again, AIC was used to compare among competing parameterizations within each taxonomic group.

Model-based predictions

Predicted densities for each taxonomic group in relation to modeled explanatory variables were generated as marginal means from the most supported model (Searle *et al.*, 1980), and bias corrected to ensure proper estimation of the lognormal mean. Arithmetic means were included in all seasonal and interannual analyses (Figures 2–6) for purpose of comparison to prior studies. However, all results for seasonal and interannual trends presented

Table 2. Summary of the significance of predictors in the most empirically supported Generalized Linear Models (GLMs) for each major zooplankton taxonomic group at the BATS site.

Taxonomic categories		Predictors								
		Yr	Mo	D/N	MT	PP	Chl	Hex	Fuc	Pr/Pr
Copepods	Calanoid	■	■	■	■	■	▒			■
	Oithonidae	■	▒		■	▒	■	■		x
	Oncaeidae	■	■	▒	■	■		■		x
	Corycaeidae	■	■	▒	▒					x
	Sapphirinidae	■	■			▒	▒	■		x
	Harpacticoid	■	■		▒					x
Crustaceans (other than copepods)	Ostracod	■	▒	■	■	■				x
	Euphausiid	■	■	■		■		■		x
	Decapod and mysid	■	■	■			■	■		x
	Hyperiid	▒	■	■		▒		■		x
	Gammarid	▒	■	■	■	■				x
	Cladocera	▒ ***	■ ***	▒ **	■ **	■ **	▒ *	▒ *		x
Gelatinous zooplankton	Chaetognath	▒	■				■	■		■
	Appendicularian	■	■		■	▒		■		x
	Doliolid	■	■	▒		▒	■	■		x
	Cnidarian	■	▒	■		▒				x
	Polychaete	■	▒	■	▒	■	▒			x
Pelagic snails	*Limacina* spp.	■	■	■		▒				x
	Other thecosome	■	■	■		▒				x
	Gymnosome	▒ * ■ **	■ ***	**	▒ *	**				x
	Heteropod	■	■	■		■				x
Selected larva	Barnacle nauplii	■	■			▒				x
	Brachiolaria	▒ * ■ **	■ ***		▒ **	▒ *				x
	Leptocephali	▒ ***	▒ ***	■ * ▒ **	■ *					x

Predictors with significant ($p < 0.05$) influence on taxa density, or presence—in the case of delta GLMs, are denoted by boxes with dark grey fill. Predictors used in the most empirically supported GLM but did not significantly ($p > 0.05$) influence taxa density or presence are denoted by light grey. White boxes represent predictors not included in the most empirically supported GLM for that taxon. Predator/prey densities were only tested in calanoid copepod and chaetognath GLMs, as denoted by the "x" in boxes for all other taxa in that predictor category. In the case of rarer taxa (cladocera, gymnosome, brachiolaria, and leptocephali) delta GLM results are noted by "*" for binomial results (rate of encounter) and "**" for lognormal results (mean density) and "***" when both binomial and lognormal results agreed. Year and Month predictors were used in all GLMs to determine seasonal and internal variability.

Yr, year; Mo, month; D/N, day/night explanatory variable; MT, mesopelagic temperature (°C); PP, primary production (mgC/m^2/d) integrated 0–140 m; Chl, chlorophyll *a* (ng/m^2) integrated 0–140 m; Hex, 19′-hexanoyloxyfucoxanthin concentration (ng/kg) integrated 0–140 m; Fuc, fucoxanthin (ng/kg) integrated 0–140 m; Pr/Pr, predator or prey density (ind./m^3).

Table 3. Summary of long-term variables of interest tested in the most empirically supported GLM for zooplankton density for five abundant taxonomic groups (calanoid copepods, ostracods, chaetognaths, appendicularians, and *Limacina* spp.), and the data sources used.

Long-term variables of interest	Source
North Atlantic Oscillation (NAO)	www.cpc.noaa.gov/products/precip/CWlink/pna/nao.shtml
Hurrell NAO (annual and winter–DJFM)	https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based
Atlantic Multidecadal Oscillation (AMO)	http://www.esrl.noaa.gov/psd/data/correlation/amon.us.data
Gulfstream North Wall (GSNW)	http://www.pml-gulfstream.org.uk/data.htm
Multivariate El Niño Southern Oscillation Index (MEI)	www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/
North Pacific Gyre Oscillation (NPGO)	http://www.o3d.org/npgo/
Pacific Decadal Oscillation (PDO)	http://research.jisao.washington.edu/pdo/
Water column stratification index (WCSI)	Density difference between 40 and 160 m averaged over the 4 months of July–October for each year, as described previously in Steinberg *et al.* (2001)
Annual mean sea surface temperature	NOAA OISST (Reynolds 25-km)
Annual mean Chl *a* concentration	http://oceancolor.gsfc.nasa.gov/
Annual mean primary production	http://www.science.oregonstate.edu/ocean.productivity/

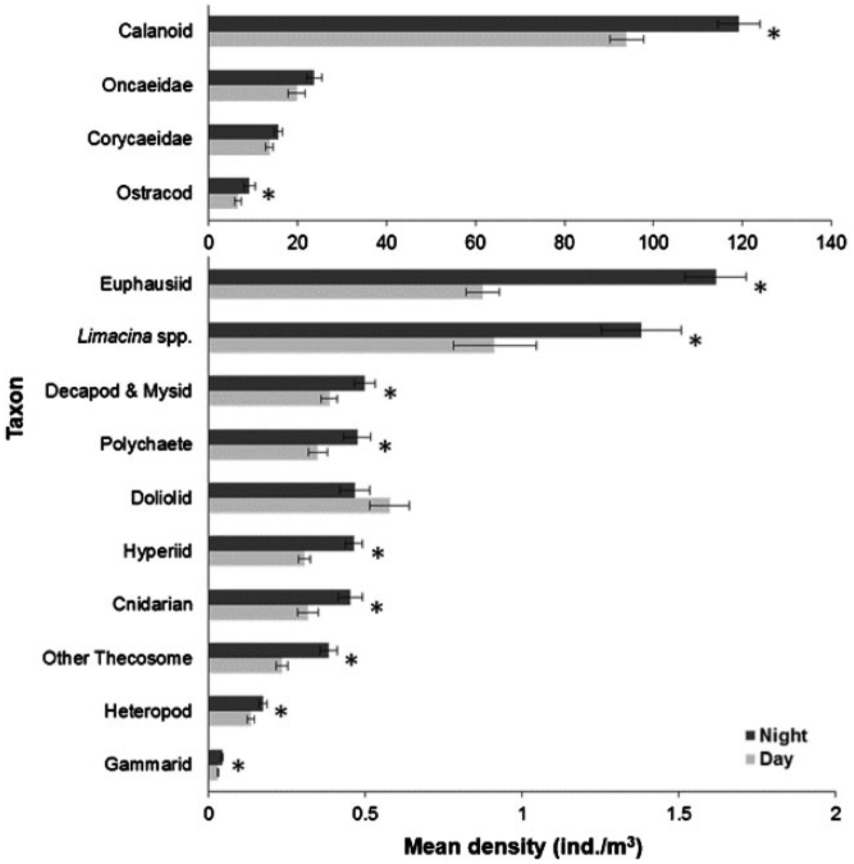

Figure 1. Mesozooplankton diel vertical migration. Day and night mean density of epipelagic zooplankton taxa at the Bermuda Atlantic Time-Series Study (BATS) site, calculated across the time series (January 1999 to December 2010). Taxa are listed in order of decreasing mean night density. Night/day parameter was included in the most empirically supported models of all 14 (non-rare) taxa. Taxa exhibiting diel vertical migration (significantly higher night density than day) are marked with an asterisk. Error bars indicate standard error.

and interpreted are based on the GLMs which accounted for this lack of normality. Standard errors of model predictions were estimated using nonparametric bootstrap resampling ($n = 1000$, Efron and Tibshirani, 1993). All statistical analyses were conducted with the software package R (version 3.2.3, R Development Core Team 2015).

Results

Diel vertical migration

Of the 24 major taxa of zooplankton examined, inclusion of the day/night explanatory variable in the AIC-based model selection was supported for 14 taxonomic groups, and for 3 additional rare taxonomic groups (presence or mean density) using the delta model (Table 2). For the non-rare taxa, 11 exhibited diel vertical migration with a significant ($p < 0.05$) higher mean density in the epipelagic zone at night than during the day (Figure 1). The strongest migrators were euphausiids, with a doubling in density at night (mean N:D = 1.9), thecosome pteropods other than *Limacina* (N:D = 1.6), both amphipod taxa (N:D = 1.5), and *Limacina* spp. pteropods (N:D = 1.5). For three groups (oncaeid and corycaeid copepods, and doliolids), the day/night variable improved overall model fit and reduced AIC, however, standard errors of the day/night parameters were large and diel differences were not significant ($p > 0.05$) (Figure 1). In rarer taxa, gymnosomes had a significantly higher mean density at night in the epipelagic zone than during the day, and leptocephali were more likely to be encountered in epipelagic zone at night ($p < 0.05$) (Table 2). The day/night variable improved the model fit for cladocera mean density, but there were no significant diel differences (Table 2).

Seasonal and interannual trends

Copepods

All groups of copepods exhibited significant ($p < 0.05$) seasonal trends except the oithonids (Figure 2a, Table 2). Calanoid and oncaeid copepod densities peaked in both winter (February–March) and summer (August). Sapphirinid copepod abundance was highest in spring (March–May), with an additional but less pronounced peak in fall (October). Harpacticoid copepod density had a distinct seasonal maxima in October. Interannual variability over the 12-year time-series was statistically significant for all copepods (Table 2). There was a distinct 2-year low density across all copepod groups in 2000 and 2001, except for sapphirinids. All copepod groups increased in abundance in 2002, leading to 1- or 2-year maxima from 2003 to 2004, with the exception of corycaeidae (Figure 2b). While there was an indication of a long-

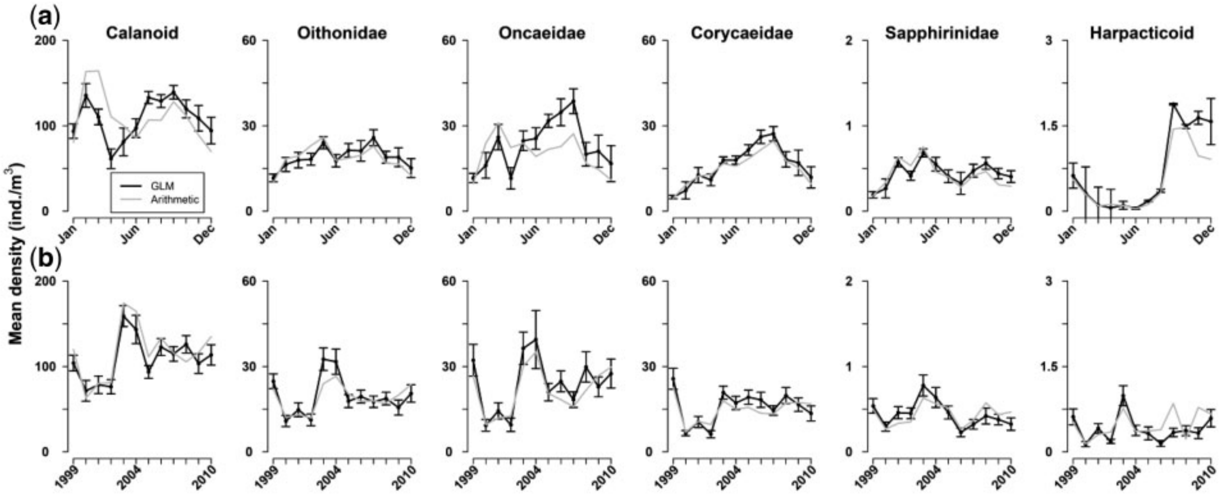

Figure 2. Mean monthly densities across all years (a) and mean annual densities across all 12 months in a given year (b) of the six major groups of copepods at the BATS site. Error bars represent the standard error of the model-based (GLM) mean. Note that in some cases the standard error bars were not plotted beyond zero.

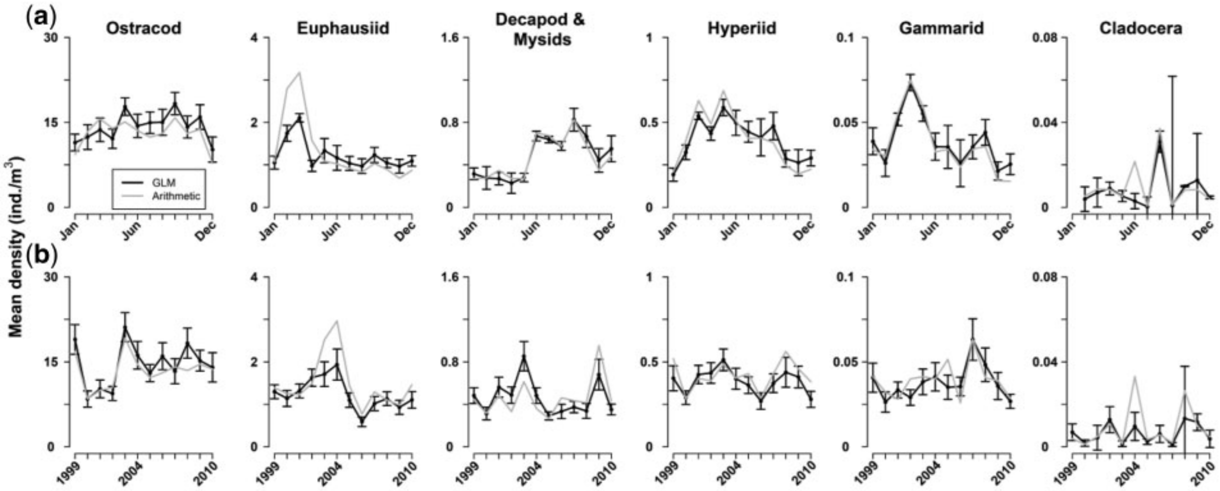

Figure 3. Mean monthly densities across all 12 years (a) and mean annual densities across all 12 months in a given year (b) of the major taxa of crustacean zooplankton (other than copepods) at the BATS site. Error bars represent the standard error of the model-based (GLM) mean. Note that in some cases the standard error bars were not plotted beyond zero.

term increase in calanoid and oncaeid copepod density over the 12-year time period, these regressions were not significant ($p > 0.05$).

Non-copepod crustacea

All non-copepod crustacea except ostracods exhibited statistically significant seasonal trends (Figure 3a, Table 2). Peaks in the spring occurred for euphausiids (March), and hyperiid (March–May) and gammarid (April) amphipods, with a secondary fall peak lower in magnitude for both amphipod groups. Decapod/mysid and cladocera densities peaked in summer (June–September and August, respectively). The grouping of "decapods and mysids" was diverse, and included *Lucifer* spp., mysids, and all decapod larvae, which may account for the broad summer/fall seasonal increase. There was a similar interannual trend amongst ostracods, euphausiids, and decapods/mysids which peaked in 2003 or 2004 followed by a decrease in abundance for the remainder of the time series (Figure 3b, Table 2).

Gelatinous zooplankton

All gelatinous zooplankton showed significant ($p < 0.05$) seasonality with peak densities in spring, and a secondary peak in the fall, except cnidaria, and polychaetes (Figure 4a, Table 2). The years 2002–2003 were a period of maximal abundance as well for appendicularians and polychaetes (Figure 4b). Doliolids and cnidarians also exhibited significant interannual variability, with a doliolid density minimum in 2008.

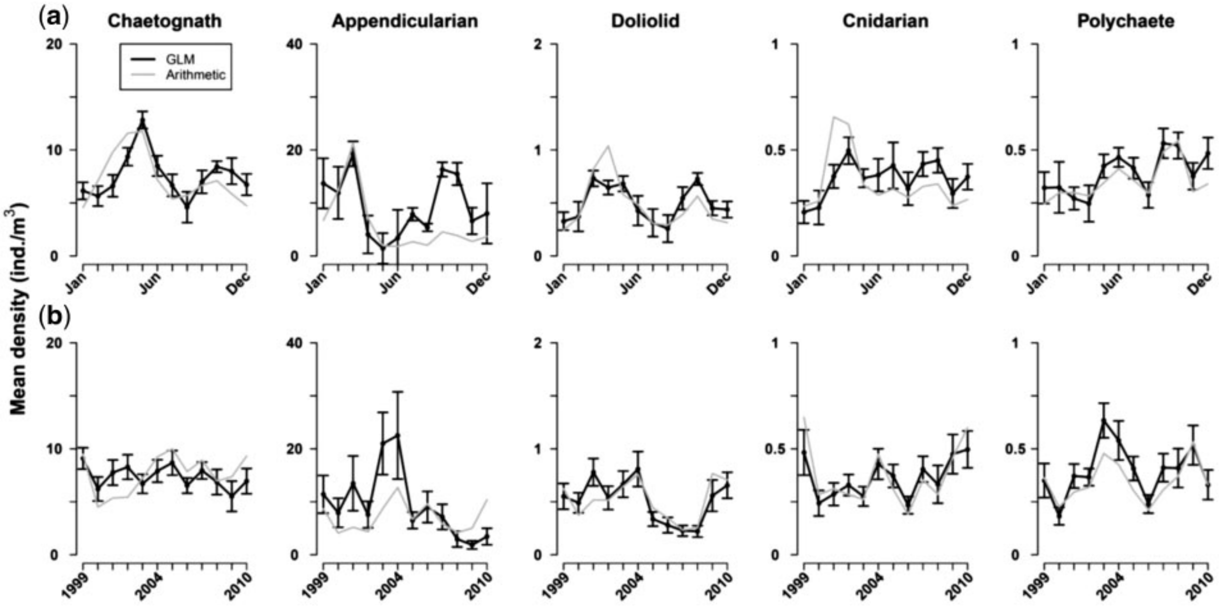

Figure 4. Mean monthly densities across all 12 years (a) and mean annual densities across all 12 months in a given year (b) of gelatinous zooplankton (chaetognaths, appendicularians, doliolids, cnidarians, and polychaetes) at the BATS site. Error bars represent the standard error of the model-based mean. Also, in some cases the standard error bars were not plotted beyond zero. Note: raw mean appendicularian data do not indicate a secondary summer/fall density maxima in (a), as the data were positively skewed and that bias was not accounted for in the raw means as it was in model-based means.

Pelagic snails (pteropods and heteropods)

The thecosome pteropod *Limacina* spp. and the heteropods exhibited two significant ($p < 0.05$) seasonal abundance peaks (May, August, respectively; Figure 5a, Table 2). Gymnosome pteropod densities peaked in fall (October) while thecosome pteropods (excluding *Limacina* spp.) showed a winter (December) abundance peak. *Limacina* spp. and other thecosome pteropods notably decreased in abundance after 2003 and 2004, respectively (Figure 5b, Table 2), with a significant long-term decrease across the time series for other thecosome pteropods (regression slope $= -0.02$, $p < 0.01$). Heteropods generally increased over the time series with progressively larger abundance peaks in 2004/2005 and in 2008. Gymnosome pteropods increased in abundance during the later years of the time series.

Selected benthic invertebrate and fish larvae

Barnacle nauplii densities were highest in winter (February), and near zero during most of the latter half of the year (June–November, Figure 6a, Table 2). Brachiolaria (sea star larvae) density was near zero during spring/summer (April–August) and completely absent in winter (February–March). Due to the low densities of leptocephali, no seasonal trend was statistically supported, however, seasonality explained enough additional variation in the data to improve the overall model fit and reduce AIC (Table 2). Barnacle nauplii abundance increased significantly across the time series (regression slope $= -0.03$, $p = 0.01$), with maximum abundance in 2008 (Figure 6b, Table 2). Brachiolaria mean annual density peaked in 2001 over the 7-year time-series (1999–2005) analysed for this taxon. Again, leptocephali were too rare to statistically support significant interannual variability (Table 2).

Environmental influences

Mesozooplankton density changes were most notably influenced by primary production, as AIC statistics supported the inclusion of the explanatory variable primary production in GLMs for 16 of 20 non-rare taxa analysed (Table 2). All 16 taxa had a positive relationship with primary production (of which 7 were statistically significant). These included herbivorous or omnivorous taxa such as calanoid and oncaeid copepods, and ostracods (Figure 7a). Another variable with prevalent (AIC supported inclusion for 9 of 24 taxa) and significantly positive influence on zooplankton abundances was the prymnesiophyte accessory pigment 19′-hexanoyloxyfucoxanthin (19′-hex; Table 2). Taxa that significantly increased in abundance with increasing 19′-hex included several copepod taxa, other crustaceans, and gelatinous groups. The shape of the response varied by taxa, with appendicularians increasing in an exponential manner and oncaeid copepods increasing linearly with increasing 19′-hex (Figure 7b). Of the rarer taxonomic groups, cladocera significantly ($p < 0.05$) increased in density with increased primary production (Table 2). Primary production influenced the encounter rate of brachiolaria and the density of gymnosome pteropods, but not significantly ($p > 0.05$; Table 2).

In two cases, due to a hypothesized predator–prey relationship, we included the abundance of another zooplankton taxon, chaetognaths, as a predictor. The inclusion of chaetognaths in calanoid copepod GLMs greatly improved the model fit, explaining 56% of deviance, as opposed to 32 or 37% of deviance when excluding the chaetognath predator and using a longer calanoid copepod time series (1995–2010), or the same time series (1999–2010), respectively. Chaetognaths had a significantly ($p < 0.05$) positive exponential-like response to increasing copepod density, with rapid chaetognath increase as calanoid densities approach 300 ind. m^{-3} (Figure 7c).

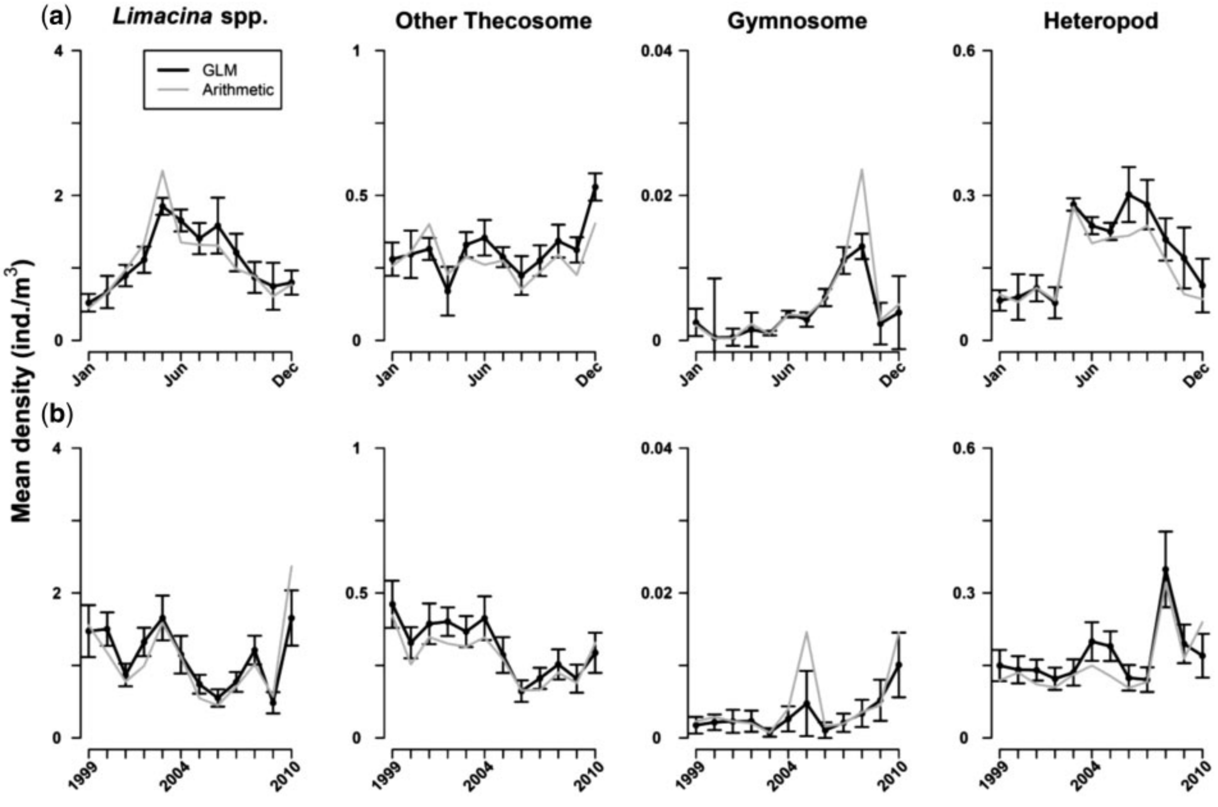

Figure 5. Mean monthly densities across all 12 years (a) and mean annual densities across all 12 months in a given year (b) of pelagic snails (pteropods and heteropods) at the BATS site. Error bars represent the standard error of the model-based (GLM) mean. Note that in some cases the standard error bars were not plotted beyond zero.

Of the remaining variables used in the GLMs, mesopelagic temperature was another common variable found across multiple zooplankton taxa, occurring in 9 of the 20 common taxa models and 4 rare taxa delta models (Table 2). Some important diel vertically migrating zooplankton like ostracods and calanoid copepods had a strong positive relationship with mesopelagic temperature (Figure 7d). Two rare taxa, leptocephali and cladocera were the only taxa that significantly decreased ($p < 0.05$) in abundance in relation to increasing mesopelagic temperature.

The remaining environmental variables evaluated for inclusion in GLMs were chlorophyll *a* and fucoxanthin. Chlorophyll *a* was present in GLMs of eight taxa and fucoxanthin was not included in any supported models (Table 2). All models with the most empirical support explained anywhere between 15 and 66% of the deviance, with the cnidaria GLM explaining 15%, and barnacle nauplii GLM explaining 66% of the deviance.

Annualized environmental and climate indices

The three top models with ΔAIC values less than 4.1 for both crustacean taxa considered (calanoid copepods and ostracods) indicated mean density is positively related to Atlantic Multidecadal Oscillation (AMO) and water column stratification index (WCSI), and negatively related to Gulf Stream North Wall (GSNW) (Figure 8a and b). Chaetognath mean density was also strongly related to WCSI, but the relationship was negative (Figure 8c). Empirically supported models for the remaining groups, appendicularians and *Limacina* spp., with ΔAIC values less than 4.1 included different predictor variables with mean density of appendicularians negatively related to chlorophyll *a* and positively related to North Atlantic Oscillation (NAO) (Figure 8d), and mean density of *Limacina* spp. negatively related to Multivariate El Niño Southern Oscillation Index (MEI) and positively related to North Pacific Gyre Oscillation (NPGO) (Figure 8e). All models with the most empirical support explained anywhere between 13 and 49% of the deviance, with the ostracod GLM using WCSI explaining 13%, and the calanoid copepod GLM using WCSI explaining 49%, of the deviance.

Discussion

Diel vertical migration

Epipelagic night:day (N:D) ratios for migrating taxa were similar to those reported for mesozooplankton inside mesoscale eddies near BATS (Eden *et al.*, 2009) and to the overall mean mesozooplankton biomass N:D ratio at BATS of 1.9 for the 1994–2010 time series (Steinberg *et al.*, 2012).The most abundant migrators in our analysis, copepods and ostracods, accounted for 94% of the total diel vertical migrator abundance, and are thus likely key components of the long-term increase in migrator biomass (73% from 1994 to 2010) reported in Steinberg *et al.* (2012). While sampling artifacts due to day time net avoidance or to patchiness are possible, mesozooplankton are mostly too small to avoid nets compared to micronekton (thus in our analyses leptocephali, euphausiids, decapod shrimps, and mysids may be more susceptible to avoidance), and when calculated across the entire 12-year data set errors due to patchiness likely do not significantly affect

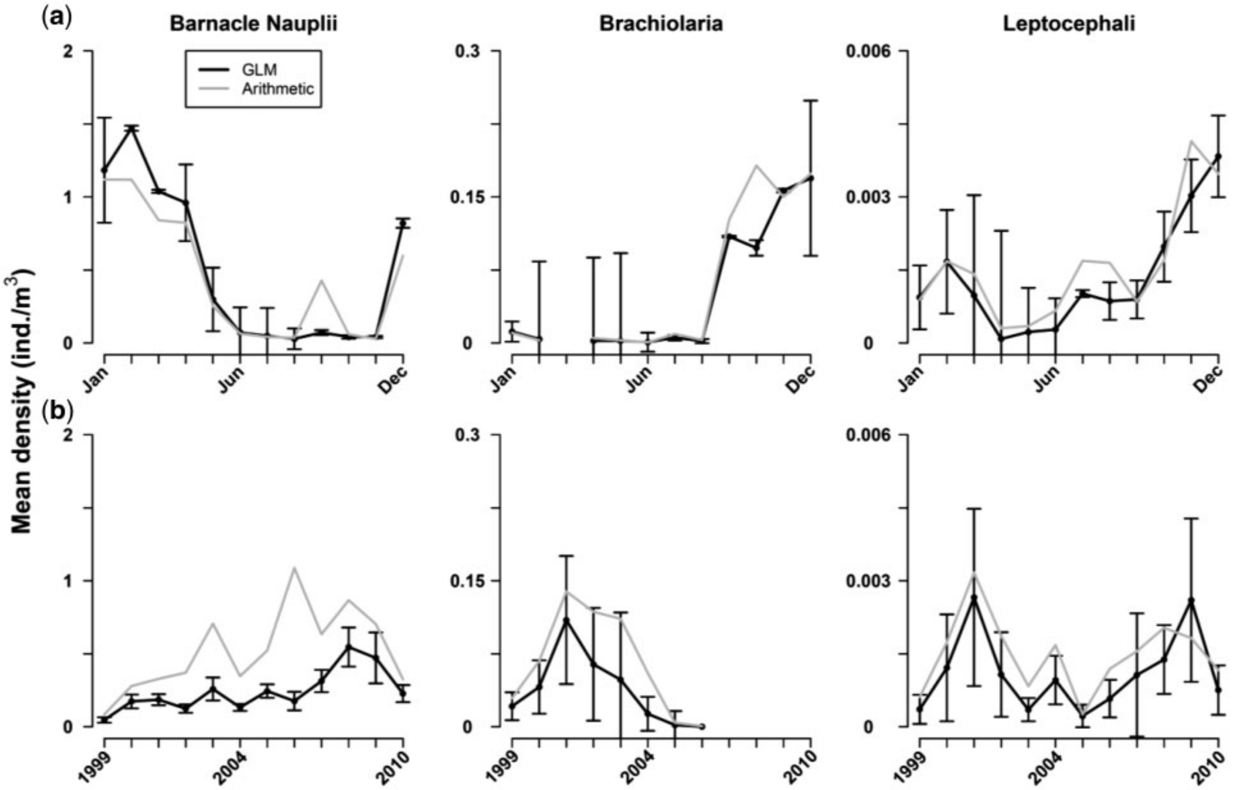

Figure 6. Mean monthly densities across all 12 years (a) and mean annual densities across all 12 months in a given year (b) of selected larval benthic invertebrates (barnacle nauplii, brachiolaria*-sea star larvae) and fish (leptocephali—eel larvae) at the BATS site. Error bars represent the standard error of the model-based (GLM) mean. Also, in some cases the standard error bars were not plotted beyond zero. *Note density of brachiolaria was not analysed for years 2007–2010, and thus these years are not included in mean monthly or annual data presented.

the overall patterns in diel vertical migration (or in other results presented below).

Seasonal trends

Copepods and other crustacea

Calanoid and oncaeid copepods, and other crustacea, such as euphausiids and amphipods, peaked following the winter/spring seasonal increase in primary production and Chl *a* biomass (Steinberg *et al.*, 2001; Lomas *et al.*, 2013). The two most abundant copepods exhibited a second abundance maxima coinciding with the secondary summer primary production increase usually dominated by picoplankton (Steinberg *et al.*, 2001). The spring February maximum in calanoid copepods occurred on average earlier (February) in the 12-year time period of our study compared to March as reported in a 14-month study by Deevey (1971) near BATS. However, in our study 4 out of 12 years also had March calanoid copepod peaks, thus we cautiously infer a phenology change.

The remaining copepod taxa exhibiting seasonality at the BATS site are more de-coupled from spring phytoplankton blooms, and rather follow seasonal changes in other prey or mesozooplankton. Sapphirinid copepod abundance may be partially tied to seasonal cycles of pelagic tunicates. Sapphirinid copepods are often associated with and regarded as predators of pelagic tunicates (Harbison, 1998; Takahashi *et al.*, 2013), and seasonal maxima of Sapphirinids co-occurred with those of doliolids in our analysis and immediately followed seasonal salp peaks observed at the BATS site from 1994 to 2011 (Stone and Steinberg, 2014). The August density maximum of carnivorous corycaeid copepods, known to prey on nauplii of copepods (Turner *et al.*, 1984, Landry *et al.*, 1985; Turner, 2004), may be timed with high prey availability during the secondary peak of copepods. The September harpacticoid copepod peak is likely tied to the summer maximum in the warm-water adapted colonial cyanobacteria *Trichodesmium* spp. (Orcutt *et al.*, 2001; Breitbarth *et al.*, 2007). Abundant harpacticoid copepods in the Sargasso Sea, such as *Macrosetella gracilis* (Andersen *et al.*, 2011), are often found associated with colonies of *Trichodesmium* which serve as a substrate and at least occasional food source for the copepods (O'Neil *et al.*, 1996; Eberl and Carpenter, 2007).

Other crustacea such as decapods, mysids, and amphipods likely contribute to the smaller secondary fall mesozooplankton biomass peak observed at the BATS site from 1994 to 2010 (Steinberg *et al.*, 2012). Although there are relatively few species of cladocera in the Sargasso Sea (e.g., *Evadne spinifera*), those that occur are known to favour warm temperatures and vertical stability (Gülsahin and Tarkan, 2012), which likely explains the very distinct August cladocera maxima.

Gelatinous zooplankton, including pelagic snails

Gelatinous zooplankton and pelagic snails generally peaked in concurrence with their food source. As reported for other gelatinous filter feeders, such as salps (Stone and Steinberg, 2014), appendicularians and doliolids have early spring maxima

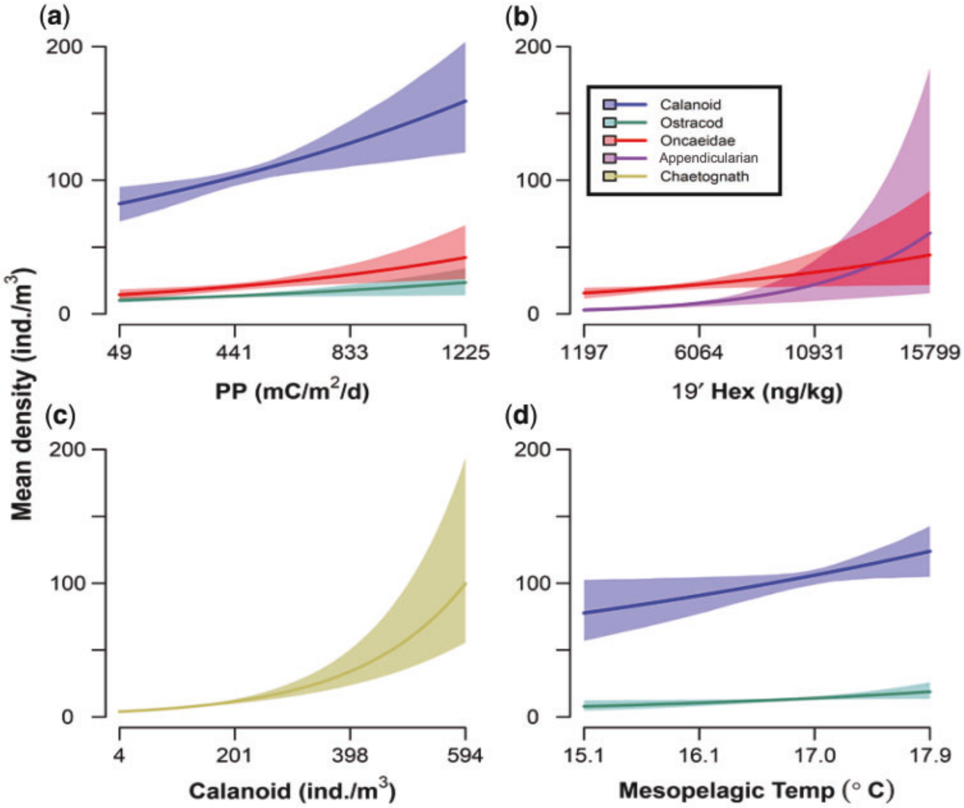

Figure 7. Short-term environmental and biological influences on mesozooplankton abundance. (a) Primary production (mC/m^2/d) integrated 0–140 m vs. abundance of calanoid and oncaeid copepods, and ostracods (ind./m^3), (b) prymnesiophytes (19′-hexanoyloxyfucoxanthin concentration) (ng/kg) integrated 0–140 m vs. calanoid copepods and appendicularians (ind./m^3), (c) calanoid copepod (ind./m^3) vs. chaetognath abundance (ind./m^3), and (d) mesopelagic temperature (°C) vs. density of two diel vertical migrating taxa—calanoid copeods and ostracods (ind./m^3). Shaded regions represent 95% confidence intervals and x-axes are labelled from the observed minimum to the observed maxima in the time series.

following the spring phytoplankton bloom at the BATS site. Carnivorous chaetognaths exhibited highest abundance following copepod (their primary prey) density maxima, and the summer heteropod maximum coincided with peaks in their common prey, shelled pteropods. Peaks in these gelatinous taxa were largely 1–2 months earlier than reported in Deevey (1971).

Benthic invertebrate and fish larvae

Barnacle nauplii had a seasonal maximum coinciding with the spring phytoplankton bloom (Steinberg *et al.*, 2001; Lomas *et al.*, 2013). Barnacles undergo multiple naupliar stages before entering the cypris stage (Høeg and Møller, 2006). Barnacle nauplii (Deevey, 1971) and depth profiles of barnacle cypriids (Eden *et al.*, 2009) have been reported in this region, but little was known of barnacle nauplii seasonal trends prior to the present work, and our findings suggest that barnacle spawning may be prevalent during winter to produce the spring maximum in nauplii.

Other larval abundance maxima did not coincide with the spring phytoplankton bloom. The high brachiolaria abundance in December may indicate a period of asexual reproduction: some brachiolaria in the BATS samples were identified as in the Oreasteridae family, which are capable of asexual reproduction, an adaptation hypothesized to allow this short-lived larva the opportunity to drift to a location suitable for settlement and increase densities to counteract high mortality rates (Jaeckle, 1994). Although seasonality in leptocephali was not statistically supported due to their low abundance, they did have periods of high abundance during cooler months of the year. Both the American eel *Anguilla rostrata* and the critically endangered European eel *A. anguilla* (Jacoby and Gollock, 2014) spawn in the southern Sargasso Sea (Andersen *et al.*, 2011). Leptocephali were present in 15% of BATS samples, with highest abundance occurring in December following the spawning season (March–July) (Jacoby and Gollock, 2014) and fall peaks of their hypothesized food sources: gelatinous zooplankton, appendicularian houses, and copepods (Mochioka and Iwamizu, 1996; Riemann *et al.*, 2010; Andersen *et al.*, 2011).

Interannual trends

The highest density increase over the 12-year time series occurred during 2003 for all six copepod taxa, three crustacean taxa (ostracods, euphausiids, decapods/mysids), and two gelatinous zooplankton (appendicularians, polychaetes). In the winter of 2003, NO_3 concentrations were at a detectable level over multiple cruises, a rare occurrence that only happened two other times (1995 and 2001) over 24 years of BATS monitoring (Lomas *et al.*, 2013). This nutrient influx likely supported the highest rate of

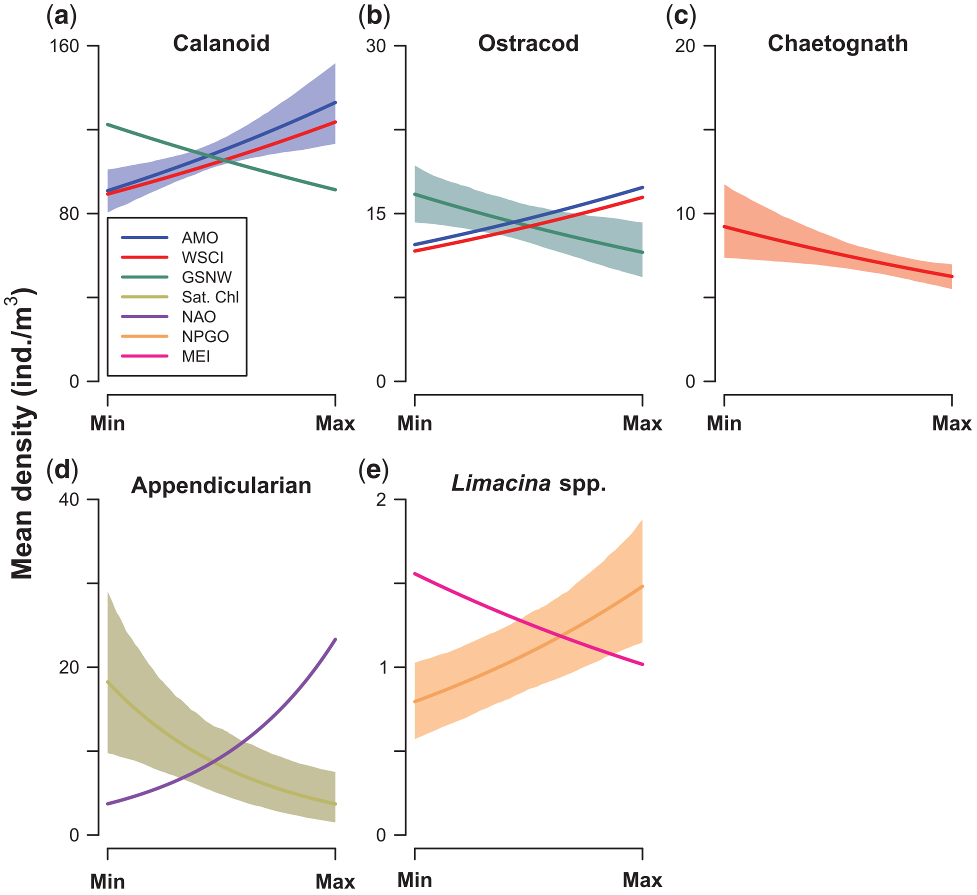

Figure 8. Mean density of abundant mesozooplankton and long-term environmental and climate indices. Note that because environmental and climate indices have different scales the data were standardized $x_{\text{std}} = (x - -x)/\sigma_x$ with minimum to maxima values listed below. Colored lines represent the Atlantic Multidecadal Oscillation (AMO) (0.3–0.35), water column stratification index (WCSI) (0.97–1.44), Gulf Stream North Wall Index (GSNW) (0.44–1.72), Satellite chlorophyll *a* (0.08–0.12 mg/m^3), North Atlantic Oscillation (NAO) (−1.15 to 0.39), Multivariate El Niño Southern Oscillation (MEI) (−0.93 to 0.58), and North Pacific Gyre Oscillation (NPGO) (−0.88 to 2.08). Shaded regions represent 95% confidence intervals of the most empirically supported longer-term variable potentially driving internal temporal changes (calanoid copepods-AMO, ostracods-GSNW, chaetognaths-WCSI, appendicularians-Chl *a*, and *Limacina* spp. pteropods-NPGO).

primary production in the time series observed in April, 2003 (1200 mg C m^{-2} day^{-1}; range for time series = 49–1200 mg C m^{-2} day^{-1}). In addition, one of three distinct diatom blooms (as indicated by a high fucoxanthin concentration of 5643 ng kg^{-1}; range for time series = 160–7863 ng kg^{-1}) also occurred in April, 2003. Thus, we posit that the majority of BATS zooplankton (about half the taxa, and comprising 96% of total zooplankton abundance in 2003) was responding (with increased growth and reproduction) to the increased phytoplankton production coupled with a rare increase in diatoms. These taxa with highest maxima in 2003 are likely driving the high positive annual anomalies of total mesozooplankton biomass that occurred from 2002 to 2004 (Steinberg *et al.*, 2012). While 2004 was not an equally productive year for phytoplankton, in 2003 and 2004 calanoid copepod and appendicularian density peaks occurred in March, 1-month later than the mean for this time series (February). This later peak would be timed to better take advantage of the seasonal spring primary production increase and may explain why 2004 was also a high density year for many zooplankton taxa.

Another year of significant abundance change across multiple taxa was 2008. During this year, heteropods and barnacle nauplii both exhibited density maxima for the time series. Interestingly, doliolids had a density minimum in 2008 and was the only taxa with a negative annual mesozooplankton biomass anomaly in the latter half of the time series (Steinberg *et al.*, 2012). The year 2008 was 1 of 3 years with diatom spikes (fucoxanthin 6390 ng kg^{-1}), but with one of the lowest annual mean rates of primary production (420 mg C m^{-2} day^{-1}; range for time series = 400–620 mg C m^{-2} day^{-1}) with the spring bloom occurring in January (520 mg C m^{-2} day^{-1}), which may explain lower abundance of other taxa and low overall biomass in that year.

There was generally a long-term increase in abundance of calanoid and onceaid copepods, ostracod, and barnacle nauplii over time. Given that copepods and ostracods make up the majority of the time-series abundance (67%), this increase may partially account for the long-term increase in total mesozooplankton biomass at the BATS site (Steinberg *et al.*, 2001). Longer-term decreases in abundance across the time series occurred in appendicularians and in *Limacina* spp. and significantly in other thecosome pteropods. GLMs indicated that long-term appendicularian abundance was positively related to the NAO index. The decrease in appendicularian density might indicate that frequent mixing conditions at the BATS site, which are associated with an increasingly negative NAO since 1996 (Steinberg *et al.*, 2012) might not be favourable conditions for this taxa. Although mixing could dilute the net-detected abundance of a common but slow swimming taxa such as appendicularians, other relatively common, slow swimming taxa did not exhibit the same relationship with NAO, suggesting an appendicularian-specific response. Variability in depth distribution of different taxa within the epipelagic zone (Eden *et al.*, 2009) and in mixing depth at BATS, which ranges from 10 m in summer to as much as 100–400 m in winter (Lomas *et al.*, 2013), may also play a role. In regards to the shelled pteropod decrease, dissolved inorganic carbon (DIC) concentrations have increased 2% and pH levels in the euphotic zone have decreased ∼0.05 over the last 3 decades at the BATS site (Bates *et al.*, 2012). Ocean acidification can reduce calcification ability of shelled pteropods (Fabry *et al.*, 2008; Bednaršek *et al.*, 2016; Manno *et al.*, 2017) and increased carbon dioxide affects pteropod metabolism (Maas *et al.*, 2016). Direct effects of increasing DIC and decreasing pH on pteropods at the BATS site has not yet been reported, but the apparent decrease in *Limacina* spp. and other thecosome pteropod densities over this 12-year period suggests that further studies of these and other environmental controls on pteropods are warranted.

Environmental influences

Primary production was the dominant environmental influence, with more than half of the 24 mesozooplankton taxa analysed increasing in abundance with increasing primary production. These include three taxa (calanoid and oncaeid copepods, and ostracods) that together account for 73% of the average zooplankton abundance in this time series. While oncaeid copepods are active predators (Go *et al.*, 1998) or detritivores (Ohtsuka *et al.*, 1993; Turner, 2004), they exhibited a similar positive relationship to primary production as ostracods, suggesting that energy transfer up the food chain at the BATS site may occur rapidly.

Only 5 out of 25 taxa studied did not show abundance changes influenced by primary production, four of which (corycaeid copepods, decapods/mysids, chaetognaths, and Leptocephali) are known/hypothesized to not be herbivorous (Venetia and Hans, 1991; Lee *et al.*, 1992; Mochioka and Iwamizu, 1996; Riemann *et al.*, 2010; Andersen *et al.*, 2011). Chaetognaths increased exponentially as calanoid copepod prey increased, and the inclusion of calanoid copepod abundance in the most empirically supported GLM for chaetognaths increased the deviance explained from 20 to 39%. These findings are suggestive of a trophic linkage although such specific trophic interactions cannot be confirmed due to the structure of these data, i.e., synoptic sampling of taxa, no time-lags in the respective series. Additional taxa with abundance not associated with community primary production were the harpacticoid copepods, presumably due to dependence of at least some harpacticoid species on *Trichodesmium* (O'Neil, 1998) as mentioned above.

Prymnesiophyte abundance (19′-hex) also had a significant and positive effect on more than one-third of the meozooplankton taxa, including appendicularians and oncaeid copepods. Prymnesiophytes, such as coccolithophorids, are the most abundant nanophytoplankton at the BATS site (Steinberg *et al.*, 2001). Appendicularian abundance increased slowly with increasing prymnesiophyte concentration until a threshold was reached after which appendicularian abundance increased rapidly. This relationship may illustrate the ability of appendicularians to rapidly respond to favourable conditions, as also seen in coastal regions (Nakamura *et al.*, 1997). Oncaeid copepods also increased in density with increased prymnesiophyte abundance. Although onceaids may not feed on prymnesiophytes directly, *Oncaea* spp. use appendicularian mucous houses as a habitat and food source (Ohtsuka *et al.*, 1993). Interestingly, the inclusion of appendicularian abundance in the most empirically supported GLM for oncaeids increased the deviance explained from 37 to 43%.

Increases in mesopelagic temperature, at daytime residence depths for vertically migrating zooplankton, could lead to increased calanoid copepod and ostracod abundance. This combined with potential increased metabolic rate at depth due to higher temperatures could result in greater active flux of carbon and nutrients by migrators below the mixed layer (Steinberg *et al.*, 2000). Conversely, another diel migrating taxon, the leptocephali, decrease as mesopelagic temperature increases. Further warming of these waters could thus affect the survival of these rare, and, in some cases, critically endangered species (Andersen *et al.*, 2011; Jacoby and Gollock, 2014).

Annualized environmental and climate indices

Calanoid copepod and ostracod long-term (12-year) density trends were significantly influenced by the AMO, GSNW, and WCS. The phase of AMO denotes long-term sea surface temperature variability and is linked to hurricane frequency in the North Atlantic (Goldenberg *et al.*, 2001; Knight *et al.*, 2006). The AMO, which is on a ∼20-year cycle, has been in a warm phase since 1996 (Goldenberg *et al.*, 2001), which causes warm sea surface temperatures and increased episodic mixing events due to increased hurricane occurrence in the North Atlantic (Goldenberg *et al.*, 2001). Thus, the positive AMO may support increased calanoid and ostracod densities because episodic mixing allows greater nutrient mixing from depth and increased primary production (Saba *et al.*, 2010).

The GSNW is used to track the movement of the north wall of the Gulf Stream and is known to correlate with the NAO with a lag of 2 years (Taylor and Stephens, 1980). A high NAO index results in a more northward path of the Gulf Stream (Taylor and Stephens, 1980). GSNW movement is related to sea surface temperature, winds, atmospheric pressure, and salinity in the North Atlantic (Taylor and Stephens, 1980). High latitude zooplankton, especially copepods, are reported to increase in abundance as GSNW moves north across the North Atlantic (Taylor *et al.*, 1992). In our study we observed both calanoid copepods and ostracods from the more southerly, subtropical BATS site region decrease in abundance as the GSNW moved north. This suggests that zooplankton in the Atlantic respond to the relative proximity of the GSNW, with increased abundance as the GSNW moves closer to the resident zooplankton. This is likely due to closer proximity of GSNW bringing local changes in mixing as a result of changes in wind speed and direction (Taylor and Stephens, 1980).

Calanoid copepods, ostracods, and chaetognath densities were influenced by the WCSI, which has been increasing over the time series and suggests a decrease in mixing and nutrient input (Steinberg *et al.*, 2001, 2012). Calanoid copepods and ostracods increased in abundance with increasing water column stability, as did total zooplankton biomass (Steinberg *et al.*, 2012) and two species of salps (Stone and Steinberg, 2014) at the BATS site. Increased net primary production observed at the BATS site from 1989 to 2007 (Saba *et al.*, 2010) suggests that stronger summer stratification over time does not affect winter mixing, which is crucial for supplying nutrients to support spring phytoplankton blooms (Lomas *et al.*, 2010, 2013), and small- and shorter-term mixing events promoted by internal waves, Rossby waves, storms, or eddies, could also inject nutrients supporting increased production (Sangrà *et al.*, 2001; Sakamoto *et al.*, 2004; McGillicuddy *et al.*, 2007). Chaetognath density decreased with increasing stratification, however, which is surprising given the strong positive relationship with their copepod prey.

Appendicularians were most strongly influenced by long-term Chl *a* concentrations and secondly by the NAO. The NAO became negative in 1996 and has continued to decline, which leads to increased mixing (Lomas *et al.*, 2010) from higher storm activity (Dickson *et al.*, 1996). This resulted in increased primary production (Lomas *et al.*, 2010), Chl *a* (Saba *et al.*, 2010), mesozooplankton biomass (Steinberg *et al.*, 2012), and abundance and biomass of *Cyclosalpa polae* (Stone and Steinberg, 2014) over the course of the time series. The relationship of appendicularian density to Chl *a* and the NAO was the opposite, which may explain the decrease in abundance observed later in the time series. A negative relationship with NAO was also seen in three of the major salp species at the BATS site (Stone and Steinberg, 2014).

Long-term *Limacina* spp. abundance was most closely linked to Pacific climate indices including the NPGO and MEI. Although the mechanism is still not fully understood, Pacific climate oscillations do appear to affect the BATS planktonic food web—as primary production (Saba *et al.*, 2010), mesozooplankton biomass (Steinberg *et al.*, 2012), salp biomass and abundance (Stone and Steinberg, 2014), and *Limacina* spp. abundance increased with increased NPGO index. *Limacina* spp. abundance also increased as MEI decreased, a relationship also noted for salps at the BATS site (Stone and Steinberg, 2014).

Summary and conclusions

Mesozooplankton seasonal and interannual cycles at the BATS site are driven by changes in local environmental conditions that are tied to larger-scale, longer-term climate control. Primary production was a leading driver of zooplankton abundance across seasons and years, with high primary production coupled with a detectable nutrient influx and diatom bloom, potentially increasing abundance of zooplankton across multiple taxa and trophic levels. Over the BATS time series primary production and total mesozooplankton biomass from 1994 to 2010 increased (Steinberg *et al.*, 2012). The possible long-term increase in calanoid and oncaeid copepod, and ostracod abundance may account for this increase, despite that the time period of this analysis (1999–2010) excluded several early years of low biomass (1994–1998) reported in Steinberg *et al.* (2012). Decreases in abundance over the time series were observed in four taxa, which may be related to increased sea surface temperatures and ocean acidification, however, further study is required to fully understand the mechanisms driving abundance decreases.

Zooplankton also play a key role in biogeochemical cycling through their feeding, metabolism, and diel vertical migration (Steinberg and Landry, 2017). We detected a significant relationship between the most abundant zooplankton migrators and mesopelagic temperatures suggesting that warming of these waters may increase efficiency of active transport of carbon below the mixed layer, but may threaten the appearance of larvae of already critically endangered species (American Eel leptocephali).

Phenology changes have been observed in the North Atlantic zooplankton (Richardson, 2008), and it is noteworthy that we found a 1-month earlier peak abundance compared to the early 1960s in multiple taxa. However, due to the limited length of the historical time series for comparison we cannot confidently infer phenological changes in those taxa.

Future analyses should further test hypothesized changes in zooplankton communities with continued warming, such as predicted size changes (shift to smaller, more tropical species). In addition, while much of this analysis was aimed at detecting bottom-up controls of zooplankton abundance, we did find evidence of top-down control that is rarely considered in oceanographic studies (Hernández-León, 2009) and that warrants further investigation. The cascading effect of changes in mesozooplankton, many of which prey upon microzooplankton (<200 μm)—the dominant grazers in the world's oceans (Schmoker *et al.*, 2013), have on primary producers (Armengol *et al.*, 2017) in this context also remains unresolved. While the mechanisms by which environmental drivers affected patterns in abundance of some of the mesozooplankton taxa in our study require further exploration, it is evident that future changes to the zooplankton community could affect the pelagic food web and biogeochemical cycling in the North Atlantic and other subtropical gyres.

Acknowledgements

We are thankful to all the dedicated staff and scientists of the Bermuda Atlantic Time-series Study (BATS), as well as the captains and crews of the R/Vs *Weatherbird II* and *Atlantic Explorer*, over the past decades. Sabrina Hood, Gabrielle Thornton, Lauren Kelly, Phoebe Robb, and especially Anjali Bhatnagar, Anna Klompen, and Josie Shawver assisted in preparing samples for microscopy and ZooScan analysis. Mark Brush and Walker Smith provided valuable feedback, and comments by Santiago Hernández-León and an anonymous reviewer improved the manuscript. We would also like to acknowledge Joe Cope, Brandon Conroy, Joshua Stone, Patricia Thibodeau, Miram Gleiber, and Sid Bosch for their technical and analytical support. Randolph Jones, Daniel Kaufman, Vincent Saba, and Marjorie Friedrichs assisted in gathering satellite data.

Funding

The BATS zooplankton time series was initially funded by National Science Foundation, USA (NSF) Grant OCE-9202336 to L.P. Madin, and continued by the BATS program through the NSF Chemical and Biological Oceanography programs (OCE-9301950, OCE-9617795, and OCE- 0326885), and through OCE-0752366 and OCE-1258622 to D.K.S., which funded this current effort. This paper is Contribution no. 3782 of the Virginia Institute of Marine Science, College of William & Mary.

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Handling editor: C. Brock Woodson